Published in final edited form as:
Neuroreport. 2011 June 22; 22(9): 413–418. doi:10.1097/WNR.0b013e3283455c23.

Hemodynamic Signals Of Mixed Messages During A Social Exchange

Nancy L. Zucker[1,2], **Steven Green**[2], **James P. Morris**[3], **Philip Kragel**[2], **Kevin A. Pelphrey**[4], **Cynthia M. Bulik**[5], and **Kevin S. LaBar**[1,2]

[1]Department of Psychiatry and Behavioral Sciences, Duke University Medical Center

[2]Center for Cognitive Neuroscience, Duke University

[3]Department of Psychology, University of Virginia

[4]Yale Child Study Center, Yale University

[5]Department of Psychiatry, University of North Carolina, Chapel Hill

Abstract

The present study used functional magnetic resonance imaging (fMRI) to characterize hemodynamic activation patterns recruited when participants view mixed social communicative messages during a common interpersonal exchange. Mixed messages were defined as conflicting sequences of biological motion and facial affect signals that are unexpected within a particular social context (for example, observing the reception of a gift). Across four social vignettes, valenced facial expressions were crossed with rejecting and accepting gestures in a virtual avatar responding to presentation of a gift from the participant. Results indicate that conflicting facial affect and gesture activated superior temporal sulcus, a region implicated in expectancy violations, as well as inferior frontal gyrus and putamen. Scenarios conveying rejection differentially activated the insula and putamen, regions implicated in embodied cognition and motivated learning, as well as frontoparietal cortex. Characterizing how meaning is inferred from integration of conflicting nonverbal communicative cues is essential to understand nuances and complexities of human exchange.

Keywords

social cognition; social rejection; biological motion; emotional expression; multisensory integration; functional magnetic resonance imaging; autism

Human interactions are rife with mixed messages. A warm smile with an unenthusiastic embrace, a hearty handshake with a wary gaze--these subtle nuances of human communication must be deciphered to derive coherent interpretations of another's intentions. While the signaling functions of facial expressions and body gestures are becoming increasingly well-established [1], it is unclear how these social signals influence the meaning of other interpersonal cues and guide inferences regarding the actions of others

Corresponding Author: Nancy L. Zucker, PhD, P.O. Box 3842, Department of Psychiatry and Behavioral Sciences, Duke University Medical Center, Durham, NC 27705 USA, zucke001@mc.duke.edu Telephone: (919)668-2281 Fax: (919)681-7347.

There are no conflicts of interest to report.

during dynamic dyadic encounters. These critical constituents of social communication often provide conflicting information that complicates the interpretation of intention. Understanding how the brain extracts meaning from discrepant nonverbal signals to arrive at higher-order inferences of motivation remains an unmet challenge of social neuroscience.

Subtleties in nonverbal expression are critical for providing context during social exchanges. For instance, eye gaze influences interpretation of intention as conveyed by facial affect [2]. Moreover, there is a reciprocal influence of body gesture and facial affect in interpreting social meaning when one of these signals is ambiguous [3]. Incongruent affective signaling between face and body expression is detected early in the visual processing stream, as reflected by increased occipital P1 amplitude [4]. An emotional 'McGurk' effect has also been reported in which prosody influences the interpretation of facial affect and vice versa, even when attention was directed to a particular sensory target [5]. This body of work supports the tendency to derive coherent interpretations of complex social stimuli even in the face of ambiguity or conflict.

Neural models of contextual expectancy violation in biological motion cues have emphasized the role of the superior temporal sulcus (STS), particularly in its right posterior aspect [6,7]. For instance, the STS is more engaged when an avatar misdirected gaze away from a visual target compared to a condition than when the gaze tracked the target appropriately [8]. The STS is also more activated when actions are incongruent with emotional context as established by facial affective displays [9], such as when an actor smiles at one object but reaches for another one. Such findings have led to theories emphasizing the role of the STS in action understanding [9].

Rejection offers a particularly salient context for studying mixed social signals. Evolutionarily ancient neural systems have evolved to rapidly detect signals of social rejection and related threat due to the potentially dangerous implications of ostracism [10]. The physical embodiment of social rejection has been substantiated in part by findings of enhanced insular activation in several related paradigms involving rejection and isolation [11], disgust [12], and social exclusion [13,14].

While violations of contextual expectancies have been examined in relation to social stimuli such as eye gaze, social gesture, and facial affect [3,8,9], it is unclear what neural regions are differentially sensitive to *mixed messages* during *dynamic* dyadic exchanges. *Mixed messages* are defined here as conflicting sequences of biological motion and affective signals that are not prototypical responses expected in familiar social contexts. In such instances, social gestures are interpreted according to expectations established by immediately preceding affective cues, knowledge of an individual's typical behavioral repertoire, or social norms established for particular dyadic exchange prototypes. The goal of the present study was to characterize neural activation when body gesture and facial affect conflicted during a familiar, dynamic social exchange. Bestowing a gift is a universal benevolent social gesture with which individuals have much prior experience and is an appropriate setting to examine brain activity in response to incongruence of affect and gesture, as individuals would have established expectations on appropriate outcomes.

Study participants offered a virtual avatar a gift. The avatar responded with one of four conditions obtained by crossing two types of facial affect (disgust or happiness) with two social gestures (acceptance or rejection). Most people would expect that individuals display positively valenced affect to the bestower and accept the gift (social *acceptance*). However, when this anticipated expression-gesture sequence is violated, our expectations are defied but in very different manners. When an offered gift is rejected but with a look of grateful appreciation, we feel socially *rebuffed*. When an offered gift is accepted but received with a

look of disgust or disdain, this is socially inappropriate and we are offended (social *faux pas*). Finally, it is possible that both the bestower and the gift itself are rejected (social *rejection*). We hypothesized that the right posterior STS would be differentially activated in conditions in which affect and gesture were incongruent, and that the anterior insular cortex would be differentially activated in conditions of social rejection.

Method

Participants

Twenty-one right-handed healthy volunteers (age range = 18 to 34; mean age = 24; 11 female) participated. All volunteers had normal or corrected vision and were screened against neurological and psychiatric illnesses by self-report. Volunteers gave written consent prior to participation and were paid $20 per hour. The Institutional Review Board of Duke University Medical Center approved this project.

Experimental design

Using the Poser 6.0 software program (Curious Labs Inc., Santa Cruz, California) (Figure 1), 4 movie clip vignettes featuring a female avatar were created. The illumination of a green light signaled the beginning of a trial for the participant and was used to synchronize time-locked averaging for data analysis. Participants were instructed to press a button when the light illuminated, which triggered an animated arm to extend towards the avatar from the point of view of the participant. This extended arm offered a gold coin to the avatar. Thus, it appeared as if the study participant was offering the avatar a gift, which was intended to strengthen the sense of interpersonal engagement from the participant's perspective. The 4 trial types were derived from the fully-crossed combination of the avatar's unfolding facial expression (happy or disgust) and hand gestures (accept or reject) in response to the gift (Figure 1). Participants were informed: "You are going to be giving a person a gift. When you see a green light, press a button. Following the button press, you will proceed to give the gift. Observe the person's response to your gift."

Participants were instructed to attend to the screen at all times but otherwise were allowed to look at the stimulus presentation in any manner they wished. Each vignette lasted 8 s, and trials were separated by an 8–12 sec jittered inter-trial interval, during which the subject viewed the avatar at rest (no motion or facial affect). This randomized viewing of the avatar figure at rest served as the baseline against which the hemodynamic activity during social interaction trials was compared. Trials were randomized within 8 different experimental runs, and the experiment contained 96 trials total (24 per condition).

Imaging

Scanning was performed on a General Electric 3 Tesla Signa EXCITE system with 40-mT/m gradients and an 8-channel head coil for parallel imaging (General Electric, Waukesha, Wisconsin). Sixty-eight high-resolution images were acquired using a 3D fast SPGR pulse sequence (TR = 500 ms; TE = 31 ms; image matrix = 256^2; voxel size = 0.9375 × 0.9375 × 1.9 mm) and used for coregistration. These structural images were aligned in the near axial plane defined by the anterior and posterior commissures. Whole brain functional images were acquired using an echo-planar imaging sequence sensitive to blood oxygenation level dependent contrast (TR = 2000 ms; TE = 30 ms; image matrix = 64^2; $\alpha = 60°$; voxel size = 3.75 × 3.75 × 3.8 mm; 34 contiguous co-planar axial slices).

Data Processing

Image processing and statistical analysis was performed using SPM8. Preprocessing was applied to individual subjects' data in the following steps: (i) spatial realignment for

correction of motion artifacts, (ii) spatial normalization to the Montreal Neurologic Institute (MNI) space using the unified segmentation and normalization as implemented in SPM8 [15], (iii) spatial smoothing using a Gaussian kernel of full-width half-maximum 8 mm, and (iv) temporal high-pass filtering. Regressors for each of the 4 trial types were modeled by convolving an 8-s boxcar function with the canonical hemodynamic response function of SPM. Contrasts for all trial types versus baseline (the avatar at rest) were created at the subject level, treating run as a fixed effect. Random-effects group level analysis were then conducted using a single 2 × 2 ANOVA full factorial design implemented in SPM, with expression (happy vs. disgust) and gesture (accept vs. reject) as factors. The model included a covariate of no interest to control for participant sex effects. This additional regressor was coded for the sex of each participant and partitioned variance related to differences in participant sex from other regressors in the model. In this way, potential sex differences did not influence the activation patterns. Contrasts of interest included main effects of expression and gesture, their interaction, and the conjunction of all four conditions of the factorial design. Contrasts of beta weights were input to one sample t-tests at a threshold of $p < .005$ uncorrected with a spatial extent of 10 voxels [16]. To control for multiple comparisons, an omnibus F test was performed on the regressors of interest and thresholded at $p < .05$ FDR corrected [17] with a spatial extent threshold of 10 contiguous voxels. The conjunction analysis was subject to the requirement that the regions were active at the FDR-corrected level in each of the 4 conditions. By conducting all analyses within a single model, the results of each contrast are significant taking into consideration the variance explained by the other contrasts and the sex covariate.

Results

The primary analysis involved the expression-gesture interaction term in the ANOVA. Consistent with hypotheses, exchanges characterized by incongruent expression-gesture sequences (relative to congruent sequences) activated the posterior STS bilaterally but with a rightward asymmetry (Table 1 and Figure 1C). This region was anterior and lateral to motion-sensitive area MT revealed in the conjunction analysis (described below). Other regions activated included the right middle temporal gyrus, and the inferior frontal gyrus and putamen bilaterally (Table 1). No brain regions showed stronger activity for congruent expression-gesture combinations relative to incongruent ones.

A secondary goal was to investigate the neural correlates of social rejection. Consistent with predictions, a contrast querying the main effect of rejecting gestures (compared to accepting gestures) revealed activation in the anterior insula (Figure 1D and Table 1). Other brain regions activated included the left putamen, left premotor cortex, and the inferior parietal lobule (Table 1). The reverse contrast revealed activity in area MT and occipital cortex, likely reflecting perceptual differences across gestures.

In general, the full factorial model was dominated by the main effect of gesture and the gesture X expression interaction. Only one brain region – the right middle frontal gyrus -- showed a main effect of expression, being greater for disgust than happy expressions. Of the four social vignettes depicted, only the social rebuff condition recruited activity greater than all other conditions combined, and this occurred in the left putamen and left inferior frontal gyrus (see Table, Supplementary Digital Content 1, which summarizes the fMRI contrasts). The conjunction analyses revealed the broader network of brain areas involved across all vignettes, including motion area MT, the cuneus/precuneus, frontoparietal cortices, and right superior temporal gyrus (see Table, Supplementary Digital Content 1, which summarizes the fMRI contrasts).

Discussion

The primary goal of the present study was to determine how the brain signals actions incongruent with expectations established by facial affect during dynamic social encounters. Consistent with our hypotheses, exchanges characterized by incongruent expression-gesture sequences activated the posterior STS. Recent work has shown that this region signals expectancy violations established by facial affect cues when observing agents interact with objects [9]. The present results extend this finding to the interpersonal domain. The STS acted in consort with other frontostriatal and temporal lobe regions upon detecting a mixed message. We speculate that activation of the right inferior frontal gyrus may reflect redirection of behavioral action tendencies initiated by facial affect upon the subsequent presentation of conflicting gestural information, consistent with its role in behavioral inhibition [18]. Other frontal lobe activations may reflect error-related processing, conflict monitoring, or proactive interference [18–20], although we note that mixed messages did not recruit canonical cognitive control circuitry, such as the dorsal frontoparietal cortices or anterior cingulate.

We also examined recent work examining neural regions that become increasingly activated as the complexity of the visual stimulus increases. Work by Mangina et al. (2009) report a distributed bi-lateral network of activity corresponding to the visual complexity of a stimulus including ventral and dorsal occipital cortex, inferior parietal lobule, and frontal eye field bilaterally [21]. This pattern of results deviates from our incongruent>congruent contrast indicating that resulting findings were not just a reflection of stimulus complexity.

A secondary goal of the study was to investigate the neural correlates of social rejection. Given the importance of affiliation to survival, models of social pain argue that interpersonal rejection should be experienced as a toxic somatosensory stimulus [10]. The contrast comparing rejecting gestures to accepting gestures confirmed our hypothesis regarding activation in the anterior insula. The insular cortex has been postulated to mediate the embodiment of affective and motivated states by integrating visceral information with conscious processes [22]. Rejection of a bestowed gift may thus rely more on somatic information to extract social implications, as this scenario is rarer to encounter and has implications for the status of interpersonal relationships. The insula was activated along with the putamen, inferior parietal lobe and premotor cortex. We speculate that the inferior parietal and premotor activations, respectively, may reflect increased reflexive attention and action preparation in response to rejecting gestures. Putamen activity may indicate greater motivated learning due to the social salience of rejection encounters. Inspection of simple effects contrasts showed that the left putamen responded more strongly to the social rebuff condition than all other conditions, perhaps because prefacing a rejecting gesture with a smile implicates rejection of the bestower rather than the gift itself. Because the avatar's reaction was contingent upon the participant's initiation of the gift exchange, the vignettes simulate instrumental contingencies involving social feedback.

Only the middle frontal gyrus was sensitive to the main effect of expression when the gesture effect and interactions were taken into account. Although the insula and putamen have been implicated in processing disgust expressions [12], gestural information was more critical for their engagement in the present task. The lack of basal ganglia activity in the main effects analyses contributes to a growing body of evidence that these areas do not merely respond to social rewards but instead signal the social value of interpersonal actions. Because the gestural information occurred last in the action sequence, it complicated interpretation of the social scene. Therefore, facial affective signaling in these regions is moderated by other relevant features of the social context.

Conclusion

Characterizing how social meaning is inferred from the neural integration of mixed communicative cues is essential to understand the complexities of human exchange, to establish a hierarchy of nonverbal signals as communication devices, and to differentiate adaptive from maladaptive social inference. The present study advances this goal by underscoring the importance of facial affect in prefacing meaning to simple gestures of acceptance and rejection in response to a universal act of benevolence. The results suggest that mixed messages are mediated by brain regions involved in biological motion perception, behavioral inhibition, and other aspects of social cognition, while rejection gestures are potent social signals that elicit systems mediating visceral monitoring and motivated learning. Clinical disorders such as autism and anorexia nervosa are characterized by styles of information processing in which local details interfere with processing of global information [23], which extends to problems with extracting global inferences from social exchange. Detailing the neural circuitry of mixed messages may provide novel targets for investigation in these conditions and form a foundation for characterizing the neural instantiation of nuanced human interaction.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

This project was supported by NIH grants K23 MH070418 and R01 MH078211 awarded to Dr. Zucker, and by a Duke Institute for Brain Sciences Research Incubator award to Drs. Zucker and LaBar.

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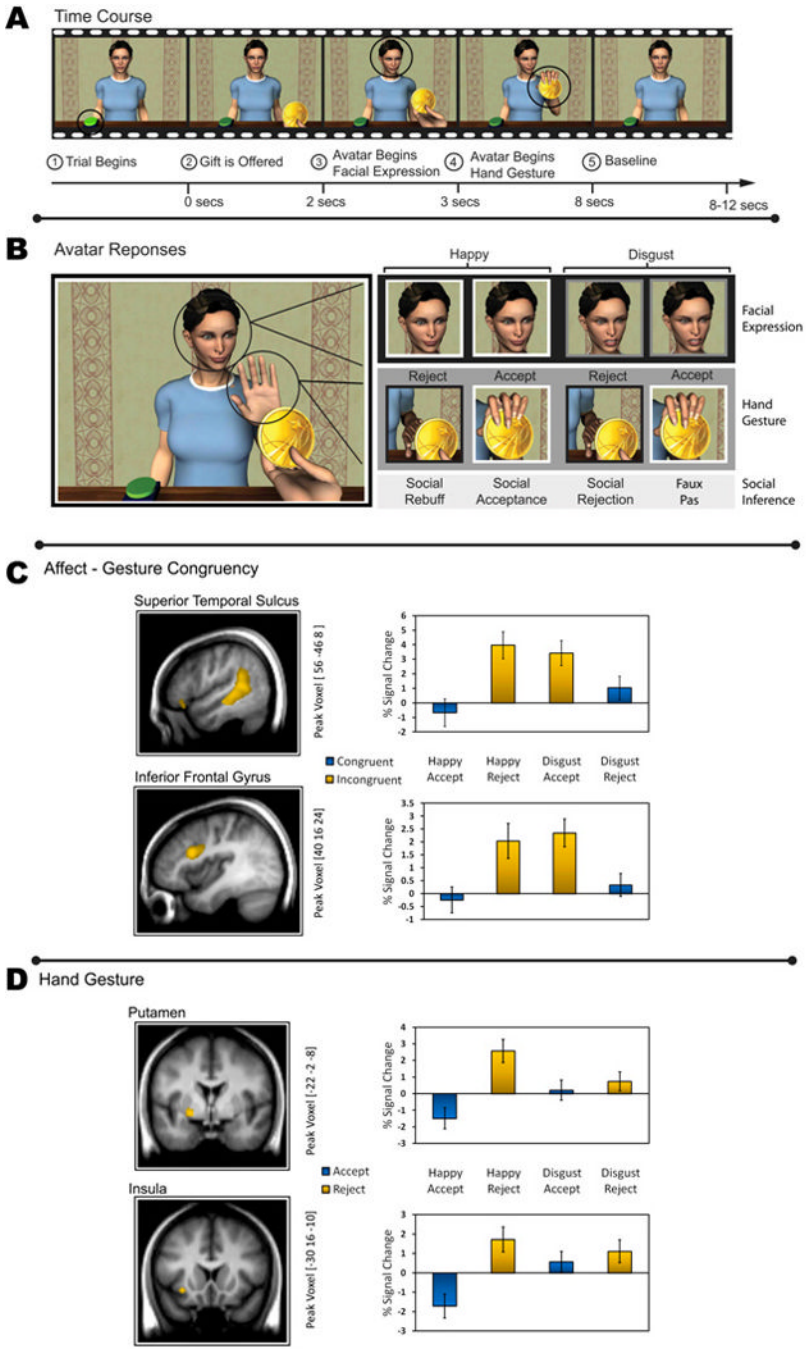

Figure.

Experimental design and representative results from the dynamic gift bestowal paradigm. A. Timeline for one trial depicting interaction sequence between participant (giver) and avatar (receiver). B. Diagram of the four experimental conditions. For each condition, the avatar expressed either positive (happy) or negative (disgust) facial affect in response to the gift, which was followed by either an accepting gesture (the coin received and kept) or a rejecting gesture (the coin knocked away). These vignettes simulated four social interchange prototypes -- social rebuff (happy/reject), social acceptance (happy/accept), faux pas (disgust/accept), and social rejection (disgust/reject). Thus facial affect and gesture were incongruent for the rebuff and faux pas conditions but congruent for the social acceptance

and social rejection conditions. C. Group parametric map showing interaction between gesture and facial affect (incongruent > congruent). The bar graph shows mean percent signal change and standard error in each of the four conditions included in the contrast for the group. D. Group parametric map showing the main effect of gesture (reject > accept). The bar graph shows mean percent signal change and standard error in each of the four conditions included in the contrast for the group.

Table 1

Gesture-Expression Interaction and Main Effects

Region	BA	Side	X_{MNI}	Y_{MNI}	Z_{MNI}	Voxel Count	Max Voxel (T-value)
Main Effect of Gesture							
Reject > Accept							
Putamen	-	L	−22	−2	−8	49	3.57
Inferior parietal lobule	40	L	−52	−50	44	99	3.45
Premotor cortex	6	L	−42	10	40	78	3.32
Insula	13	L	−30	16	−10	19	3.12
Accept > Reject							
Middle occipital gyrus	19	L	−50	−76	8	2196	5.01
Middle temporal gyrus (area MT)	21	R	46	−70	2	912	4.60
Middle occipital gyrus	19	R	36	−90	0	18	2.78
Main Effect of Expression							
Happy > Disgust							
Premotor cortex	6	R	38	6	64	66	3.35
Disgust > Happy							
No significant activations	-	-	-	-	-	-	-
Interaction of Expression by Gesture							
Incongruent > Congruent							
Superior temporal sulcus	22	R	56	−46	8	1690	4.21
Inferior frontal gyrus	45	R	40	16	24	441	4.10
Middle temporal gyrus	21	R	46	−42	8	31	3.67
Putamen	-	R	16	2	6	143	3.47
Putamen	-	L	−16	2	6	151	3.42
Inferior frontal gyrus	45	L	−40	22	22	102	3.23
Superior temporal sulcus	22	L	−58	−48	12	162	2.96
Inferior frontal gyrus	47	R	50	32	−6	73	2.84
Congruent > Incongruent							
No significant activations	-	-	-	-	-	-	-